

**PRIMORDIUM FORMATION IN HYDROPSUS SUBALPINUS
(TRICHOLOMATALES, BASIDIOMYCETES)**

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Hydropus subalpinus is exocarpic amphiblemate. The pubescence of the stipe is a cauloblema that sometimes forms a spurious partial veil in young primordia. The pileoblema becomes a gelatinised pileipellis with a few more or less erect cells on the pileus and a few layers of periclinal physalohyphae on the pileus margin. The stipe and pileus contexts are sarcodimitic, and the morphogenetic function of the physalohyphae during the expansion of the stipe and the pileus is discussed, based on specimens with an aborted sarcodimitic structure. The carpogenesis of *Hydropus subalpinus* is similar to that of *Hydropus anthidepas* and *Baeospora myosura*.

The genus *Hydropus* (Kühner) ex Singer contains about 100 species of mycenoid, collybioid or omphalinoid gilled fungi with sarcodimitic stipe trama composed of spindle-shaped, strongly inflated physalohyphae and very thin, often tortuous generative hyphae. Most species are tropical (Singer, 1982); only six or seven species occur in Europe (Moser, 1983). On inspection with a hand lens, an overwhelming number of species show no trace of a veil, not even in young basidiomes, and are thus considered gymnocarpic. However, very young fruit-bodies of *Hydropus omphaliniformis* Singer show a fugacious, silky veil connecting the margin of the pileus with the stipe (Singer, 1982: 40). This species is therefore considered to be hemiangiocarpic (Singer, 1982: 13) or monovelangiocarpic (Singer, 1986: 415), but no detailed study was made to back up Singer's statements.

Cornier (1966: 185) gives a more detailed description and schematic drawings of the development of the tropical *Hydropus* ('*Trogia*') *anthidepas* (Berk. & Broome) Singer and concludes that it shows "a very slight, false veil over the incurved pileus margin". Nevertheless he calls this species gymnocarpic.

Species occurring in temperate regions have never been studied. Bas (1999: 166), probably based on Singer (1986), writes "development gymnocarpic or monovelangiocarpic", while Watling & Turnbull (1998: 131) write "development unknown", probably referring to European species only.

Mid May 2003 many basidiomes of *Hydropus subalpinus* (Höhn.) Singer developed on buried branches of *Fagus sylvatica* in a mixed forest north of Lausanne, Switzerland. All developmental stages, noduli, primordia and young basidiomes were present on the same branches and allowed study of the primordium formation of this species.

MATERIAL AND METHODS

Forty-five noduli and primordia were fixed within 30 minutes of collection in a cacodylate buffered solution of glutaraldehyde and formaldehyde at 3–5°C for 40 hours, dehydrated with methoxyethanol, carried over ethanol and propanol into butanol for long-

time storage at about 4°C (Feder & O'Brien, 1968). Thirty-six noduli and primordia were embedded in a 7 : 3 mixture of glycol methacrylate and butyl methacrylate and serial sectioned with a microtome. The 5–8 µm thick sections were stained with 0.01% basic fuchsin in distilled water or with aluminium zirconium haematoxylin (Cléménçon, 2000). Selected sections were photographed with an Olympus DP11 digital camera mounted on a Leitz Ortholux microscope, and the photographs were prepared for printing using Adobe Photoshop on a Macintosh computer (magnification, picture cropping and contrast were adjusted, small impurities were brushed away, but no morphological changes were made).

Voucher specimens of this collection of *Hydropus subalpinus* (Höhn.) Singer are deposited in LAU under the access number HC 03/004.

RESULTS

Development of the primordium

A summary of the early development of *Hydropus subalpinus* is shown in Fig. 1 & 2. The erumpent nodulus (Fig. 1a) is hemispherical, but noduli may also be more spherical (Fig. 4a). Noduli soon become conical by apical growth (Fig. 1b). Later the apex enlarges to form the pileus rudiment (Figs. 1c, d). The pileus and the stipe become covered with a floccose metablema (Figs. 1d–f, 1i), but later the pileus becomes smooth again, as the pileoblema is transformed into a gelatinous pileipellis (Figs. 1g, h, j–l). In normally developing specimens the stipe becomes enlarged and conical, and the pileus is broadly convex to rounded-conical; but in aborted specimens the stipe remains cylindrical and the pileus becomes bell-shaped or parabolic (Fig. 1m). This is due to the absence of laterally exerted pressure because the turgescens sarcodimitic structure does not develop. About one third of all studied primordia showed this type of abortion.

Four representative developmental stages are shown in Fig. 2: a nodulus with beginning elongation and early cauloblema (Fig. 2a); a young primordium with the pileus initial, the first pileoblema, and the onset of the differentiation of the sarcodimitic structure in the stipe (Fig. 2b); an intermediate stage with a smooth prehymental palisade and the cauloblema forming a temporary partial veil (Fig. 2c); and an older primordium with well-developed sarcodimitic stipe context, beginning sarcodimitic structure in the pileus, well-developed, anticlinal pileoblema and stipitoblema, early gills and basal hyphal cords (Fig. 2d).

The vegetative mycelium in the substrate (wood of *Fagus sylvatica*) is quite sparse, each wood cell containing only very few hyphae; but where noduli are formed, the density of hyphae in the wood becomes very high just beneath the wood surface (Fig. 3). A dense mycelial mass composed of parallel hyphae ruptures the wood surface and grows out to produce a nodulus (Figs. 4a, 5a, 6, 7). Noduli may be formed on top (Figs. 4, 5) and on the sides of a buried *Fagus* branch (Fig. 6).

Noduli have a denser core surrounded by a loose outer layer (Figs. 4b, 5b). The hyphae in the base and in the lower part of the nodulus are intertwined while showing a general longitudinal orientation. They are more irregularly arranged in the upper part and in the loose outer layer. All hyphae are thin-walled. The part buried in the wood consists mainly of inflated hyphae, perhaps a means of breaking the wood surface by

pressure; but in the nodulus itself, significant hyphal inflation has not yet occurred. Noduli grow out vertically to produce a shaft of intertwined but generally longitudinal hyphae. When a nodulus is located on a horizontal surface of the *Fagus* branch, a conical body is formed, as shown in Figs. 1b and 5a. Noduli located at the vertical side of the *Fagus* branch also grow out vertically, so that the shaft is upright, parallel to the wood surface and forms a right angle with the basal mycelial mass bursting out of the wood (Fig. 6).

Primordium formation begins with the growth of a vertical shaft composed of ascending, but slightly interwoven, thin hyphae (Figs. 5a, b). Since the shaft has a smaller diameter than the nodulus the resulting body is conical with a rounded apex. From the sides of nodulus and the shaft inflated hyphae grow out and form a floccose metablema; but when a surface touches a foreign body or the soil, no metablema can grow. Therefore the occurrence and form of the metablema is very irregular in primordia growing within the soil. The apex of the primordial shaft is often covered with a very thin, compacted layer, probably the result of the pressure of the growing shaft against the soil. This layer can be called a primordial cortex.

When the length of the primordial shaft reaches about one or two quarters of the diameter of the nodulus, a pileus rudiment is initiated (Fig. 6). The apical context becomes more irregular, and hyphae grow outward in a curved line. The surface hyphae of the pileus initial are slightly inflated like the ones of the shaft metablema. Over the pileus margin they form a compact periclinal layer curving down and growing toward the shaft surface, but on the apex they are usually less compacted and may even produce some erect end cells. At this stage no prehymental palisade is present under the margin of the pileus initial.

With the onset of pileus formation, some hyphae in the nodulus and primordial shaft begin to expand by turgescence. They are the future spindle-shaped physalohyphae of the sarcodimitic stipe context. Because of this hyphal expansion the stipe initial becomes even more conical.

When the pileus reaches a diameter of about 500–600 μm , a prehymental palisade is already well formed, but gill initials are still lacking (Figs. 7, 8). In the stipe trama some hyphae begin to inflate enormously, forming spindle-shaped physalohyphae. In the centre of the pileus the physalohyphae are arranged irregularly, but towards the pileus margin they take a radial orientation. Therefore, the pileus trama also becomes sarcodimitic.

The hyphae of the upper part of the floccose metablema on the stipe grow obliquely upward in direction of the pileus margin, and sometimes they reach it (Fig. 9). But as the pileus expands more rapidly than the metablema grows, the false veil thus formed is of short duration.

At the underside of the pileus gills begin to grow down from the prehymental palisade. The young gill trama is divergent (Fig. 10a), but the descending hyphae are not parallel when seen in a section parallel to the hymenium (Fig. 10b). In this stage, the pileoblema is often well-developed and forms a floccose layer of erect hyphae (Figs. 2d, 11).

In older primordia the gill trama contains physalohyphae (Fig. 12a). The primordial hymenium consists of slender, club-shaped cells and big, vesicular cystidia (Fig. 12b). The gill trama and a thin layer between the pileus trama and the gills are partly or wholly gelatinous. The stipe elongates and thickens considerably through the inflation of the

physalohyphae that become the dominant structures by volume. The hyphae of the pileoblema run parallel to the pileus surface with some more or less erect, club-shaped end cells towards the pileus margin. Over the centre of the cap the pileoblema is strongly gelatinous (Fig. 13a). The thickness of the gelatinous layer decreases toward the cap margin and the number of free end cells increases (Figs. 13b, c). The margin itself is dry.

The stipe base sometimes contains crystals of unknown composition (Fig. 14a). In some specimens the crystals are so numerous as to form an opaque cloud; in others only a few isolated crystals can be seen. The crystals are surrounded by a thin, irregular layer of a material staining brown-red with zirconium-haematoxylin and vinaceous red with toluidine blue, indicating a polysaccharide (Fig. 14b).

Young primordia lack a strigose basal mycelium. About the time when the pileus initial appears, hyphal cords begin to grow out from the basal part of the nodulus. This is clearly visible in Fig. 1d. These hyphal cords do not develop significantly until the primordium begins to grow gills. They radiate from the stipe base and are composed of thin, cylindrical, almost parallel, vegetative hyphae only (Fig. 15). Rarely a hyphal compartment contains some deuteroplasm (Fig. 15c).

The structure of the stipe and pileus trama of older primordia

The sarcodimitic structure in the sense of Vellinga (1998) is evident in the stipe, the spindle-shaped physalohyphae being up to 20 μm wide, with compartments up to about 1800 μm long. They develop from longitudinal generative hyphae by increase of their diameter and length without significant increase of the cytoplasm, which becomes highly vacuolated (Fig. 16). The hyphal cells are multinucleate; some compartments, although incomplete in the sections, show 8 nuclei. The walls of the physalohyphae are slightly thicker than the walls of the accompanying generative hyphae and take a more pronounced red-brown colour when stained with zirconium-haematoxylin, indicating a firmer wall. It is difficult to measure the walls with the light microscope, but image analyses with the computer indicate a wall thickness of 0.20–0.24 μm , compared to 0.12–0.15 μm for the walls of nearby generative hyphae. In the bottom of the stipe the physalohyphae are irregularly arranged and often contorted, but in the upper part they are straight and more or less parallel. A sarcodimitic structure is also seen in the pileus, but here the physalohyphae are irregularly arranged. (Fig. 17). Many physalohyphae are terminated with a free ending upper cell reminiscent of acrophysalides (Figs. 16a, 18–20). The generative hyphae of the stipe are 3–5 μm thick and frequently ramified. Lateral branches wind their way between the physalohyphae (Fig. 21). They are clamped and binucleate, and are the typical ‘hyphes connectives’ of Fayod (1889) and Kühner (1938), presumably increasing the mechanical cohesion of the stipe context.

The development of the hymenial cystidia

The cystidia of mature basidiomes of *Hydropus subalpinus* were described by Kühner (1938, as *Mycena subalpina*) as being “atténuées supérieurement ou contractées en un col cylindrique” and by Watling & Turnbull (1998) as “narrowly lageniform with a subobtuse to obtuse apex ...”. Both descriptions fit my own observations of the cystidia

of this fungus which is common in my collecting sites (Fig. 23). I have never seen any other type of cystidium in mature basidiomes of this species, but in young primordia broadly vesicular cystidia with a rounded apex are common (Figs. 10a, 11a, 12b).

In older primordia, the broadly vesicular cystidia of neighbouring gills often meet at or near their apices, and together they bridge the gap between the gills (Figs. 22a, b). It is possible that the bridging cystidia have a similar morphogenetic function as the trabecular cystidia in *Coprinus* species, as described by Chiu & Moore (1990, 1993), but positive evidence is missing for *Hydropus*. Since in mature basidiomes all cystidia are lageniform and no dead or shriveled cells are present in the hymenium, it is probable that the vesicular cystidia of the primordium change their form when the gills separate during maturation.

Aborted primordia without sarcodimitic context

About one third of the primordia studied were aborted specimens, characterised by a non-dilated, about cylindrical stipe and an excessively incurved pileus margin (Figs. 1m, 24). Although aborted, they were not entirely dead. They consisted of narrow, often contorted hyphae embedded in a gelatinous mass, but the spindle-shaped physalohyphae were totally lacking in the stipe and pileus trama (Fig. 25). Aborted primordia failed to differentiate the sarcodimitic context. It is possible that the gelatinous mass containing the narrow, contorted hyphae results from the disintegration of the physalohyphae.

Obviously the stipe remains cylindrical because there are no physalohyphae to extend the stipe trama. The same is true for the pileus that becomes bell-shaped instead of conical. The pileus margin curls strongly because it is covered by normally inflated hyphae that presumably exert an inward pressure that is not compensated for. Therefore, it seems reasonable to assume that the striking physalohyphae of the sarcodimitic context are a major morphogenetic factor.

Most aborted primordia were infested with nematodes, but the cause of abortion is unknown.

DISCUSSION

So far the only other *Hydropus* species studied in some detail is *Hydropus anthidepas* (Berk. & Broome) Singer (Corner, 1966: 185, as *Trogia anthidepas*). *Hydropus subalpinus* and *H. anthidepas* are both amphiblemate, but the fate of the pileoblema is different in the two species. In *H. anthidepas* it remains dry and forms a pruinose layer of erect cells; and "hyphal ends on the pileus may grow out ... [and] may meet excrescent hyphae form the stem or primordial disk and build a very slight, false veil over the incurved pileus margin" (Corner, 1966). In *H. subalpinus* the pileoblema becomes an ixocutis bearing only a few, scattered, more or less erect cells; and no hyphae grow out to meet the cauloblema. Thus, *H. anthidepas* is slightly amphicleistoblemate in my terminology (Cléménçon, 1997), whereas *H. subalpinus* is fleetingly caulocleistoblemate, or does not form any partial veil in some specimens.

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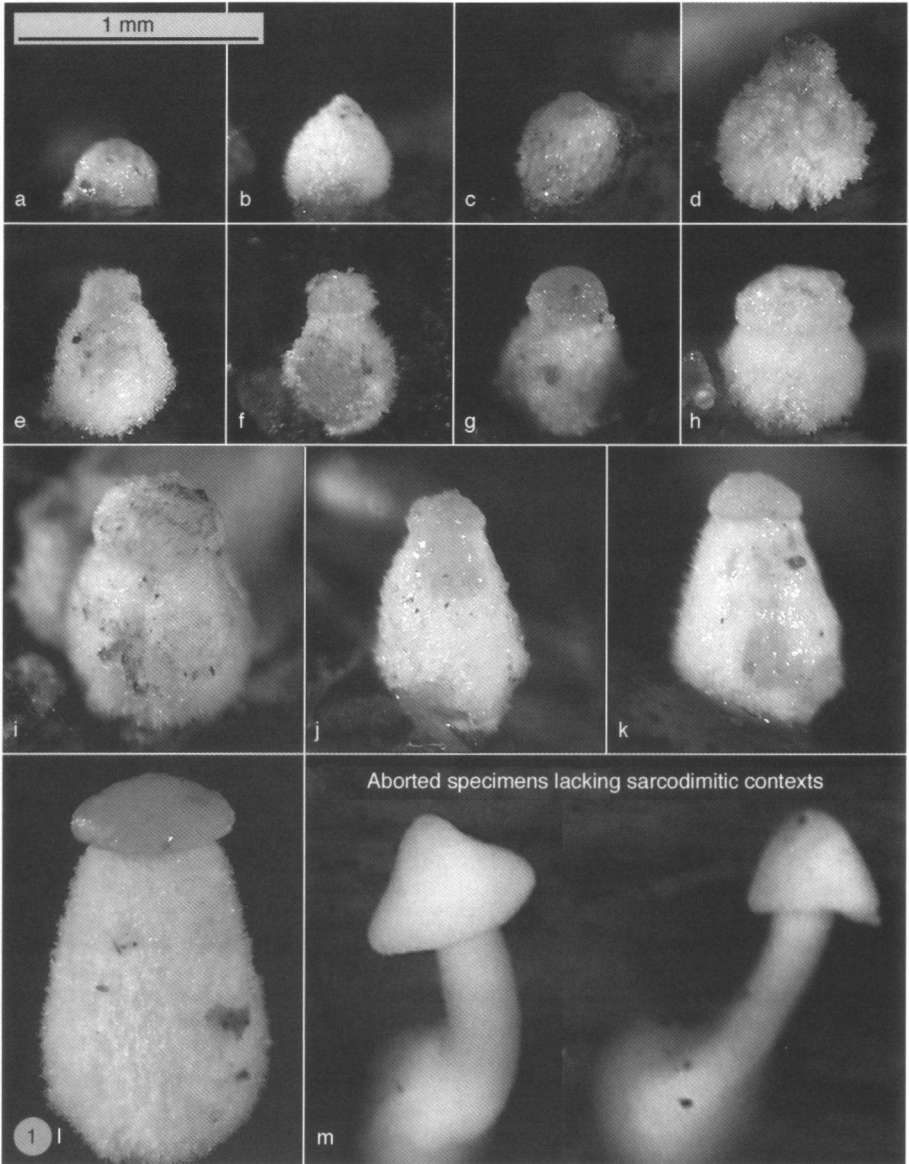


Fig. 1. Early stages of primordium formation of *Hydopus subalpinus*, from a hemispherical nodulus (a) to a young primordium with a conical stipe and a well-developed pileus rudiment (l). Note the pileoblemma (1d, e, f, i, j) and the cauloblemma (1d–l). Aborted primordia with cylindrical stipes and bell-shaped or parabolic pilei are frequent (1m). All photographs show living specimens.

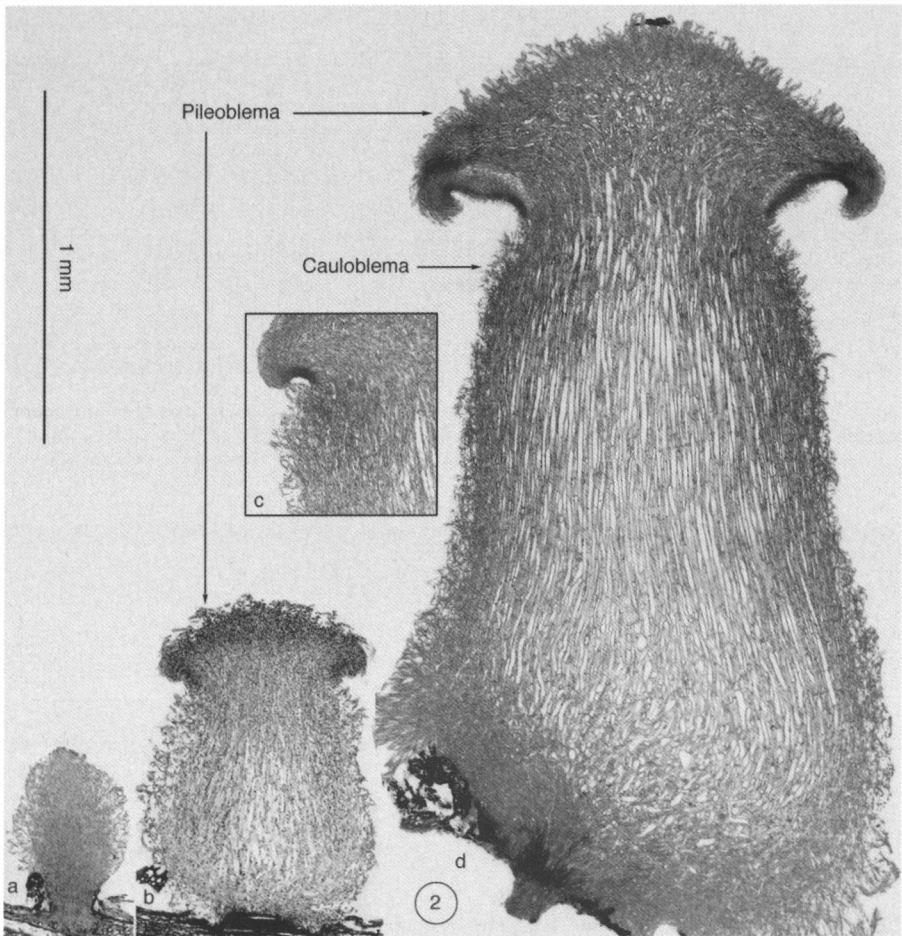


Fig. 2a–d. Four representative stages in the development of *Hydropus subalpinus* shown at the same magnification; a. The nodulus has begun shaft formation. On its sides the floccose outgrowth of the future cauloblemma is clearly visible; b. the small primordium shows a well-developed pileus initial with a downward growing margin and a young pileoblemma. On the underside of the pileus margin a prehymental palisade is in its early stages. The pileitrama lacks inflated hyphae, but they are present in the stipe that has begun to expand laterally. The sarcodimitic stipe trama is not fully developed yet. The cauloblemma is well-developed; c. a smooth prehymental palisade and a temporary partial veil produced by the cauloblemma are present; d. this primordium has a fully developed sarcodimitic stipe trama, and in the pileus some hyphae have begun to inflate. The pileoblemma is fully developed and consists of short erect hyphae; the cauloblemma consists of erect, ramified hyphae. Under the pileus the gills started to grow downward. The thin mycelium plug at the base was originally sunken into the wood substrate, but the primordium has become detached during processing. Hyphal cords grow out from the stipe base, but they are truncated in this photograph. The substrate is slanted, but the primordium is vertical.

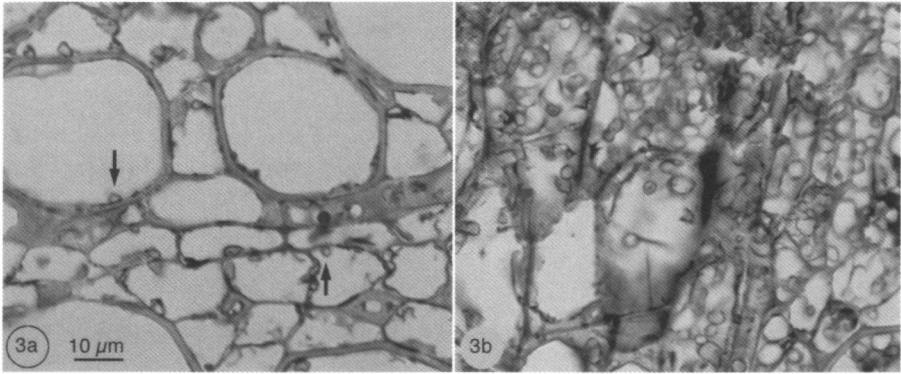
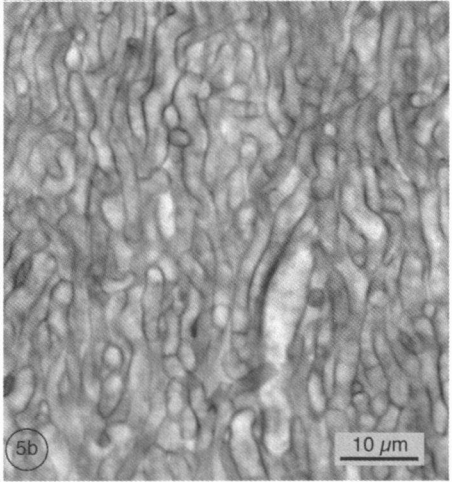
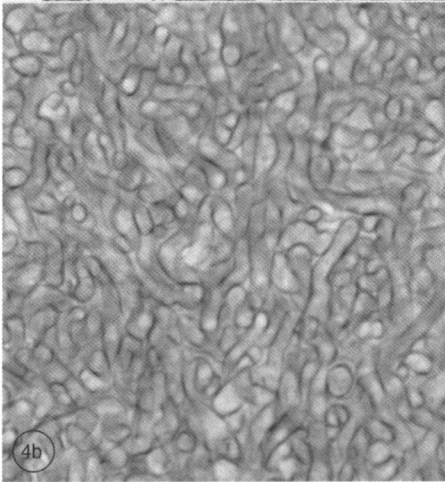
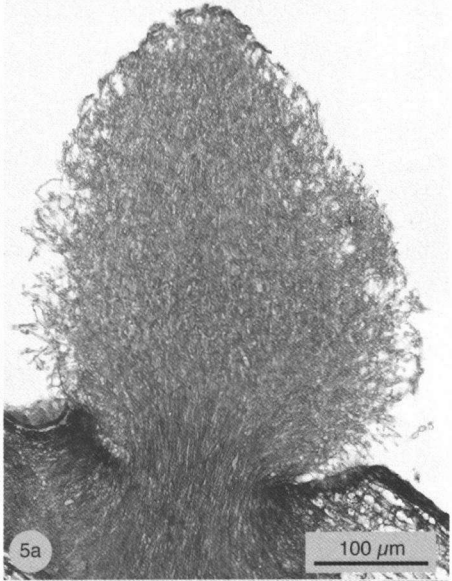
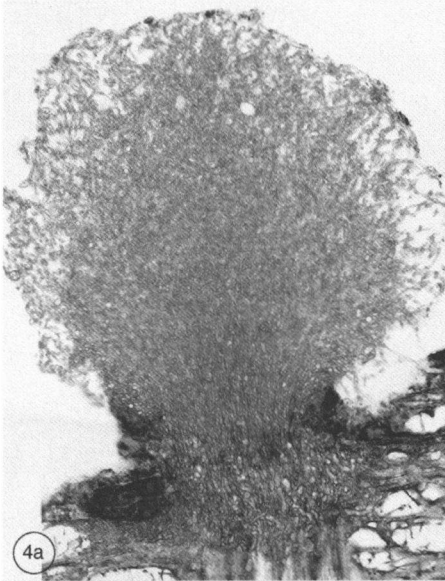


Fig. 3. Paucity of the vegetative mycelium in the beech wood (a) and abundance of the mycelium beneath a nodulus (b) of *Hydropus subalpinus*.

Figs. 4 & 5. Two noduli of *Hydropus subalpinus* developing on a mycelial mass composed of parallel hyphae breaking through the wood surface. — 4. a. A younger nodulus still about spherical. The primordial shaft has just begun to form, making the metablema initial thinner at the apex; b. irregular context in the centre of the same nodulus. — 5. a. An older nodulus with a slightly more developed primordial shaft making the nodulus more conical; b. more regular arrangement of the hyphae in the beginning primordial shaft. Some hyphae begin to inflate.



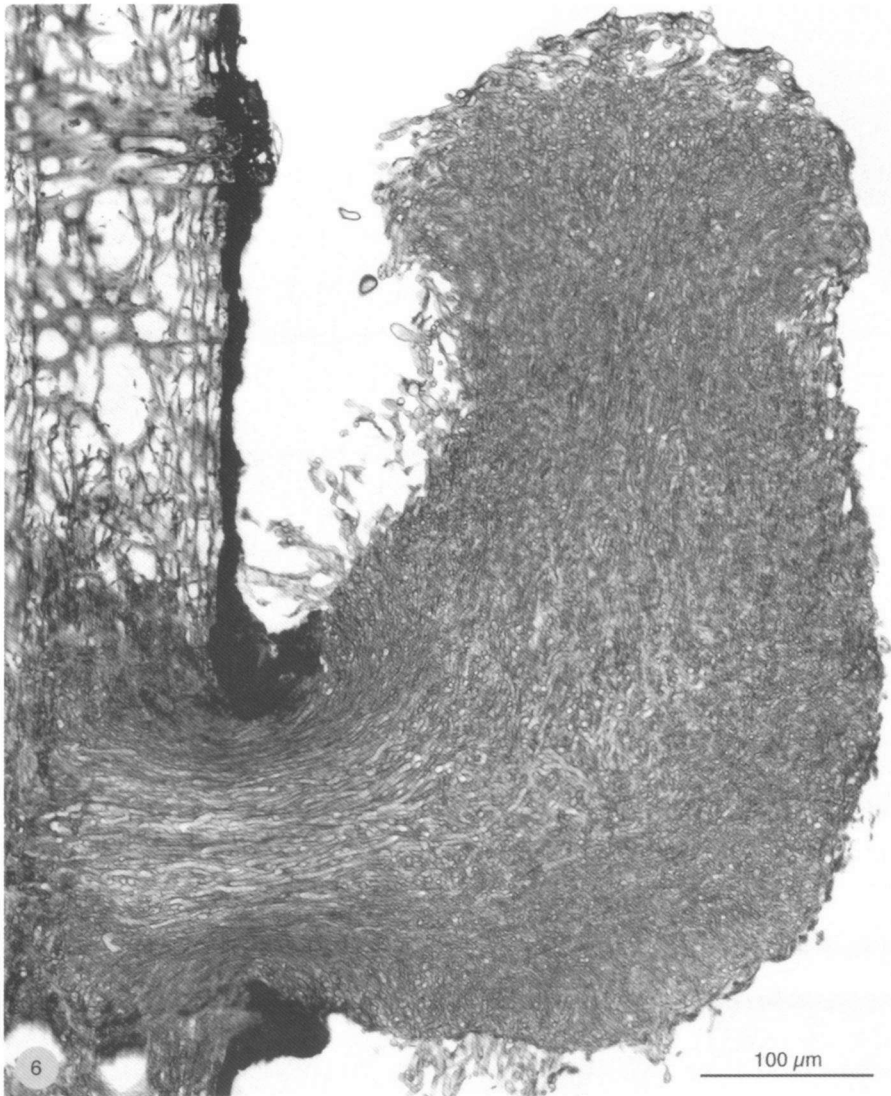


Fig. 6. A young primordium attached laterally to its rooting base that was horizontally breaking out of the vertical surface of the substrate. The nodulus is the swollen base of the stipe. Its hyphae have just begun to inflate somewhat. In the vertical shaft, the hyphae generally have a longitudinal direction but are slightly intertwined. On top of the shaft a pileus rudiment has formed by divergent hyphal growth. In the space between the substrate and the primordium a loose, floccose layer has formed, but at the right side, the surface of the primordium is exposed to the surrounding soil and has become slightly compacted. Such a layer can be called a primordial cortex.

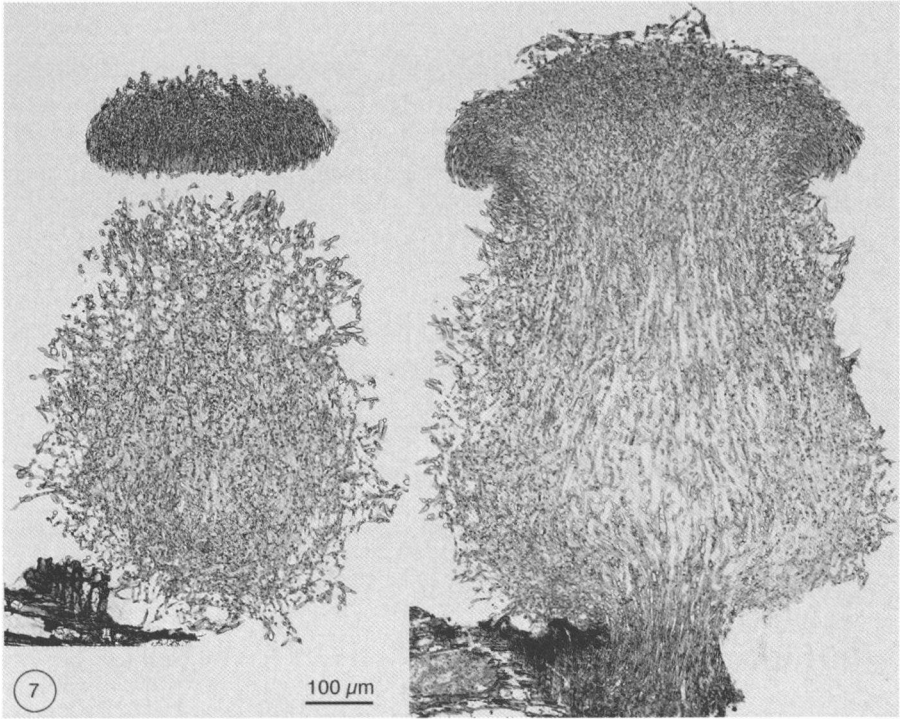
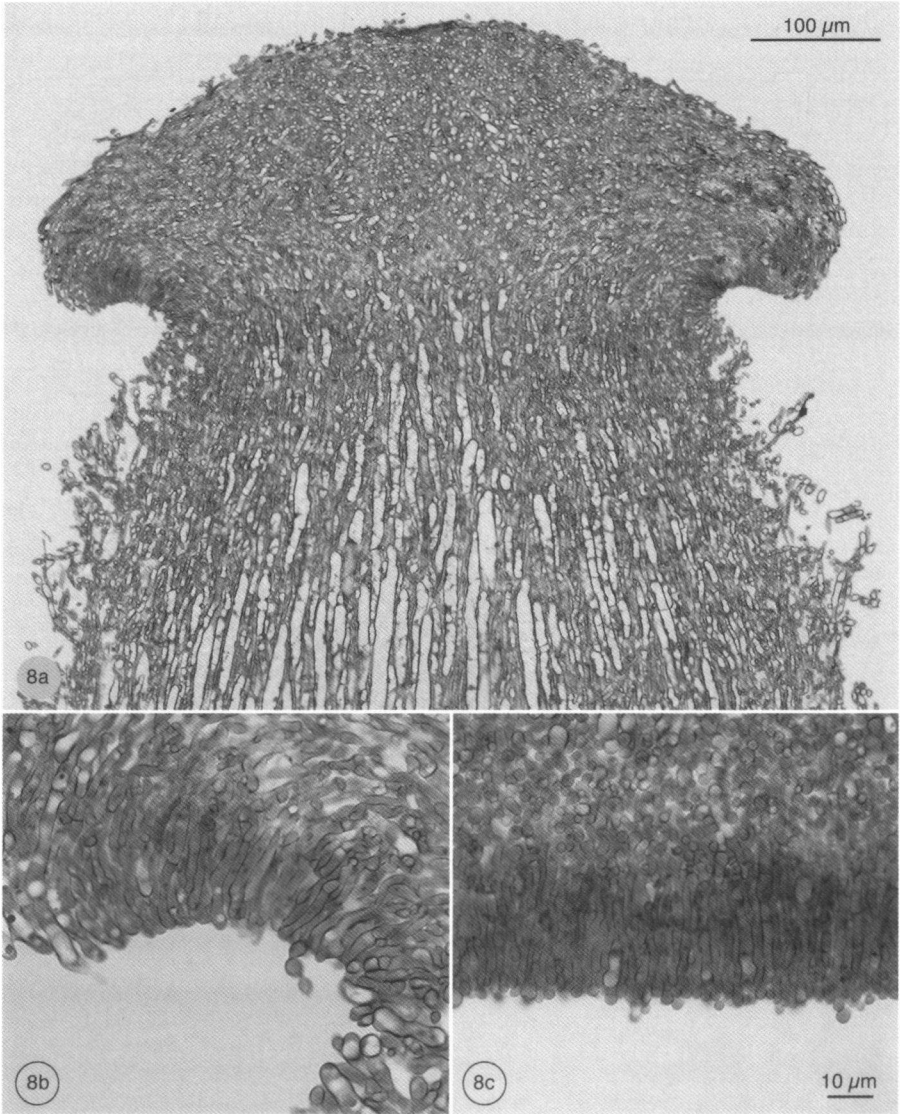


Fig. 7. Tangential and median longitudinal sections through a young primordium with a well-developed pileus initial bearing a smooth prehymental palisade at its underside. Both metablemas are well-developed and not gelatinous. The stipe trama contains some inflated hyphae, but the pileus trama does not. The mycelial plug at the base of the primordium is sunken into the wood substrate, but at the right-hand side, the substrate became detached during processing.



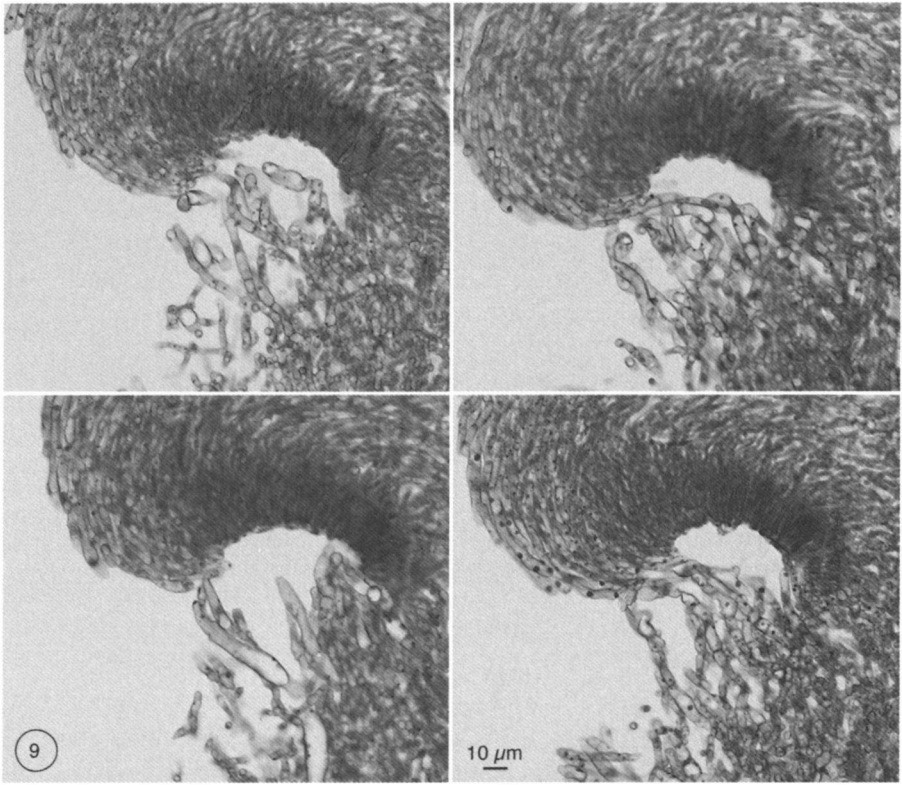


Fig. 9. Four sections from the same primordium showing the temporary formation of a partial veil by the cauloblema. This was observed in a single primordium only, so this stage may be of short duration or not present in every specimen.

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Fig. 8. a. A slightly older primordium with a more pronounced pileus shows already a much reduced pileoblema, probably due to narrow contact with the surrounding soil. The sarcodimitic structure of the stipe context is well-developed, but in the cap, some hyphae are just beginning turgescence; b, c. radial and tangential sections through the prehymental palisade that is slightly curved but remains smooth.

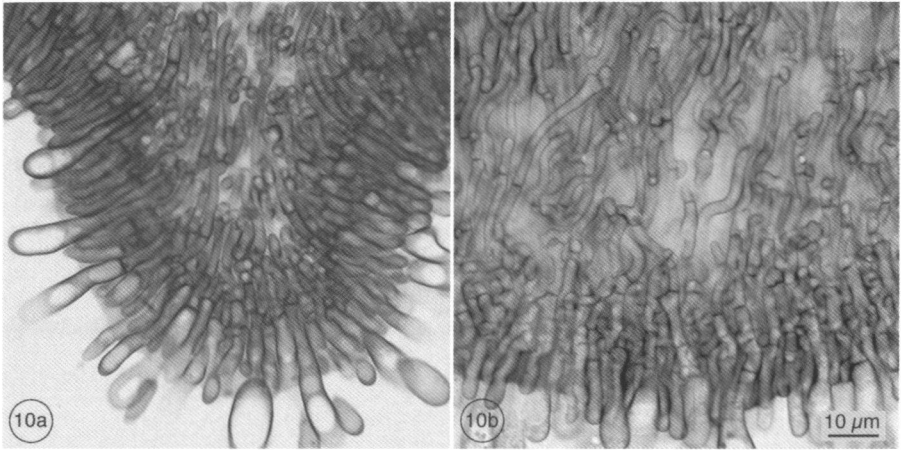


Fig. 10. Beginning of gill formation in a primordium with a cap 1.4 mm in diameter. a. In a cross-section the hyphae are seen to be divergent; b. a section parallel to the hymenium shows the hyphae to be loosely and somewhat irregularly arranged. The young gill trama is gelatinous, but this is not visible in these photographs. The hymenium consists of young basidia and bigger cystidia.

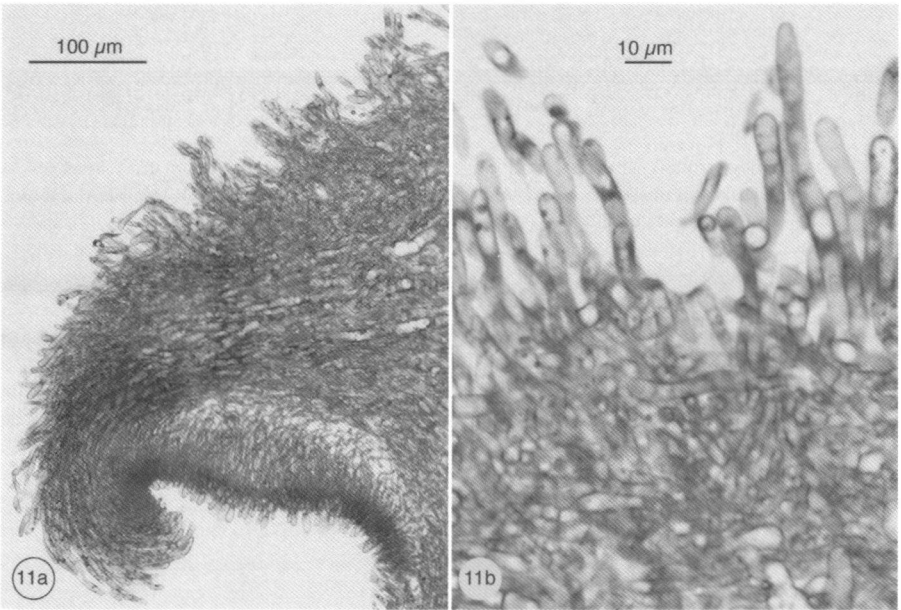


Fig. 11. Same primordium as in the Fig. 10, median longitudinal sections. a. The young gill is sectioned in its median plane and shows the down growing hyphae. Numerous cystidia on the gill edge. The pileolema is strongly developed and shows the transition from anticlinal hyphae on the upper part of the pileus to the periclinal hyphae over the cap margin. It is not yet gelatinous. Some turgescent hyphae are visible in the pileus trama; b. detail of the pileolema.

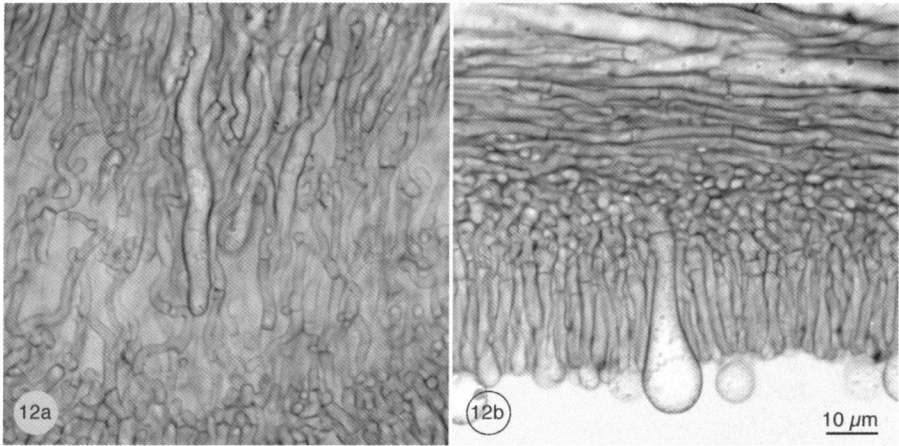


Fig. 12. Hymenophoral trama and subhymenium of a primordium with a cap 2.0 mm wide. a. Median section parallel to the hymenium showing irregularly down-growing hyphae similar to the ones in Fig. 10b, and the presence of physalohyphae; b. radial section of the pileus between two gills. The subhymenium is densely cellular. The hymenium is composed of young basidia and bigger cystidia.

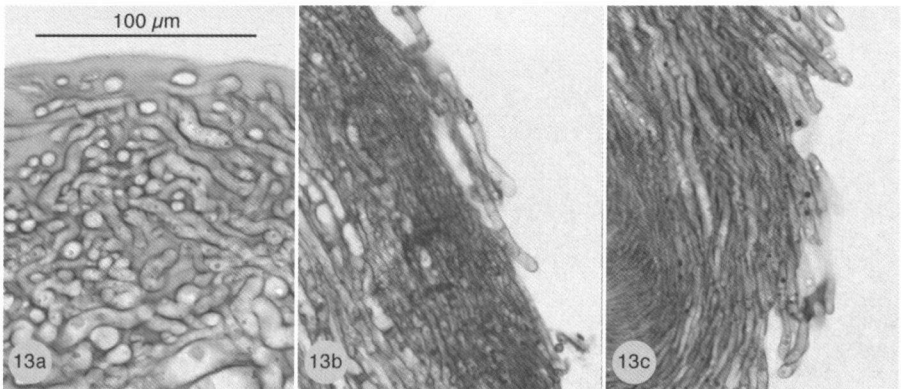


Fig. 13. Pileolemma of the primordium of Fig. 12. Transition from the gelatinous pileus apex to the dry pileus margin. a. Xocutis with periclinal hyphae; b. on the side of the cap the pileolemma consists of repent hyphae and is only slightly gelatinous. Some barely erect end cells are present. This architecture results from a re-orientation of the originally anticlinal hyphae of the pileolemma; c. the cap margin in covered with dry periclinal hyphae with erect end cells.

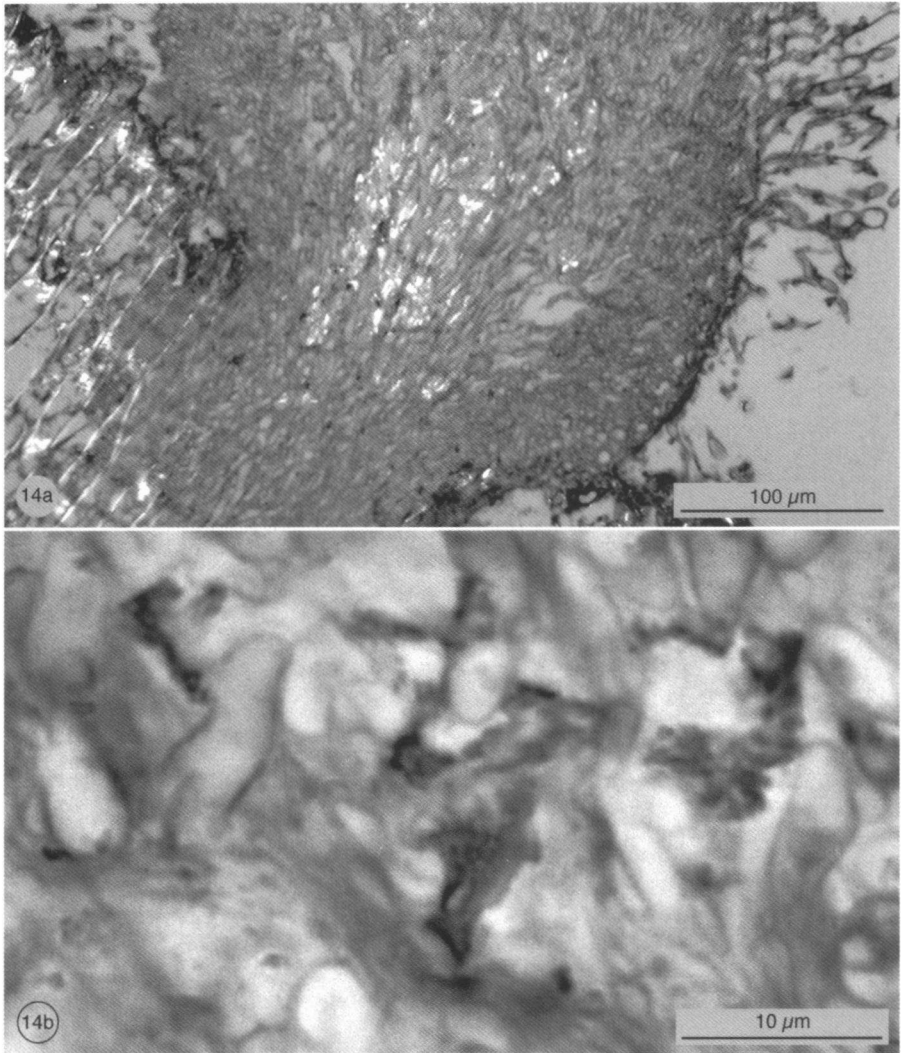


Fig. 14. a. Crystals in the stipe base of a primordium shown here in not quite crossed polarising filters. They do not occur in every primordium. The walls of some wood cells are also birefractive; b. amorphous material staining brown-red with zirconium-haematoxylin and vinaceous red with toluidine blue, indicating a polysaccharide, occur in the stipe base of some primordia. Chemical nature and biological significance of the crystals and the amorphous material are unknown.

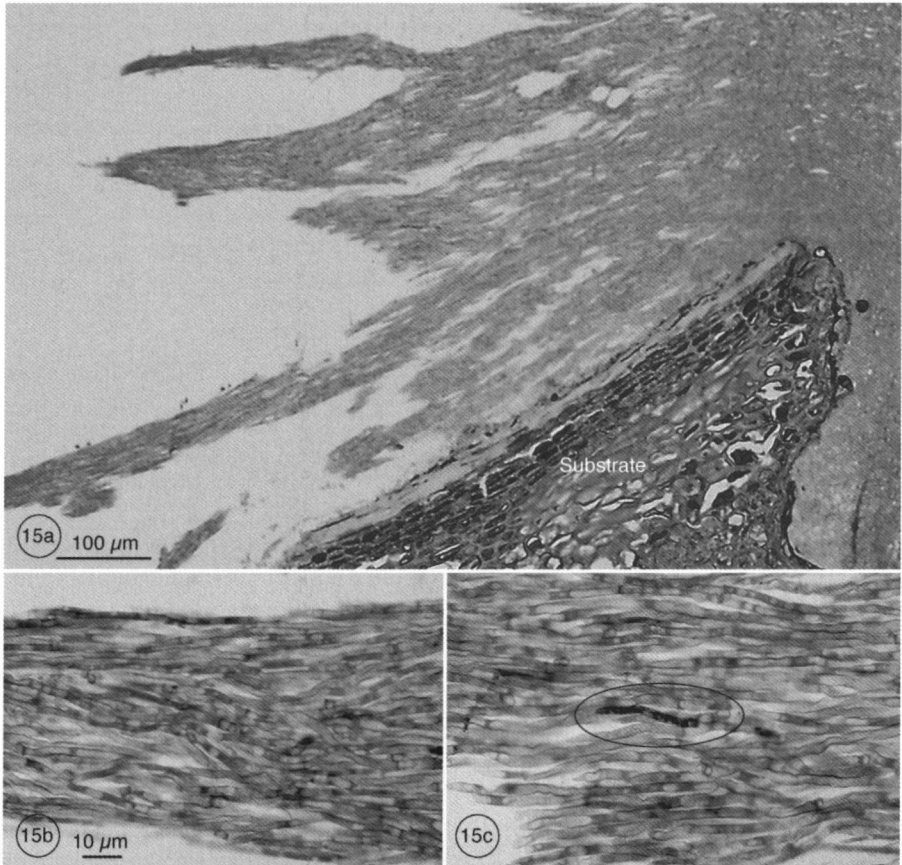


Fig. 15. Hyphal cords at the base of the stipe of an older primordium. **a.** Low power photograph of a longitudinal section. In the lower right corner the mycelial plug in the substrate; **b, c.** longitudinal sections through two hyphal cords. The ellipse in 15c indicates a hyphal cell with deuteroplasmic content.

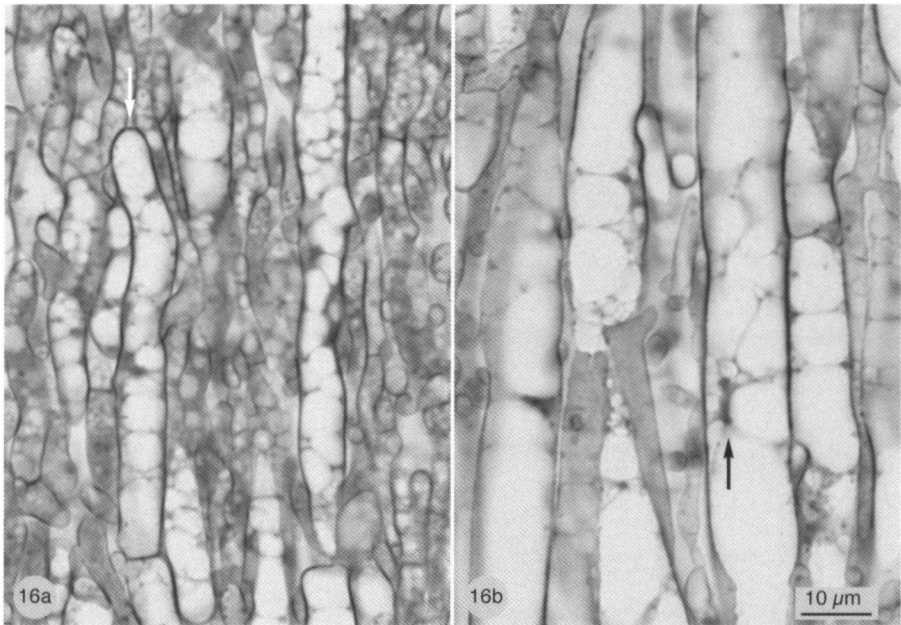
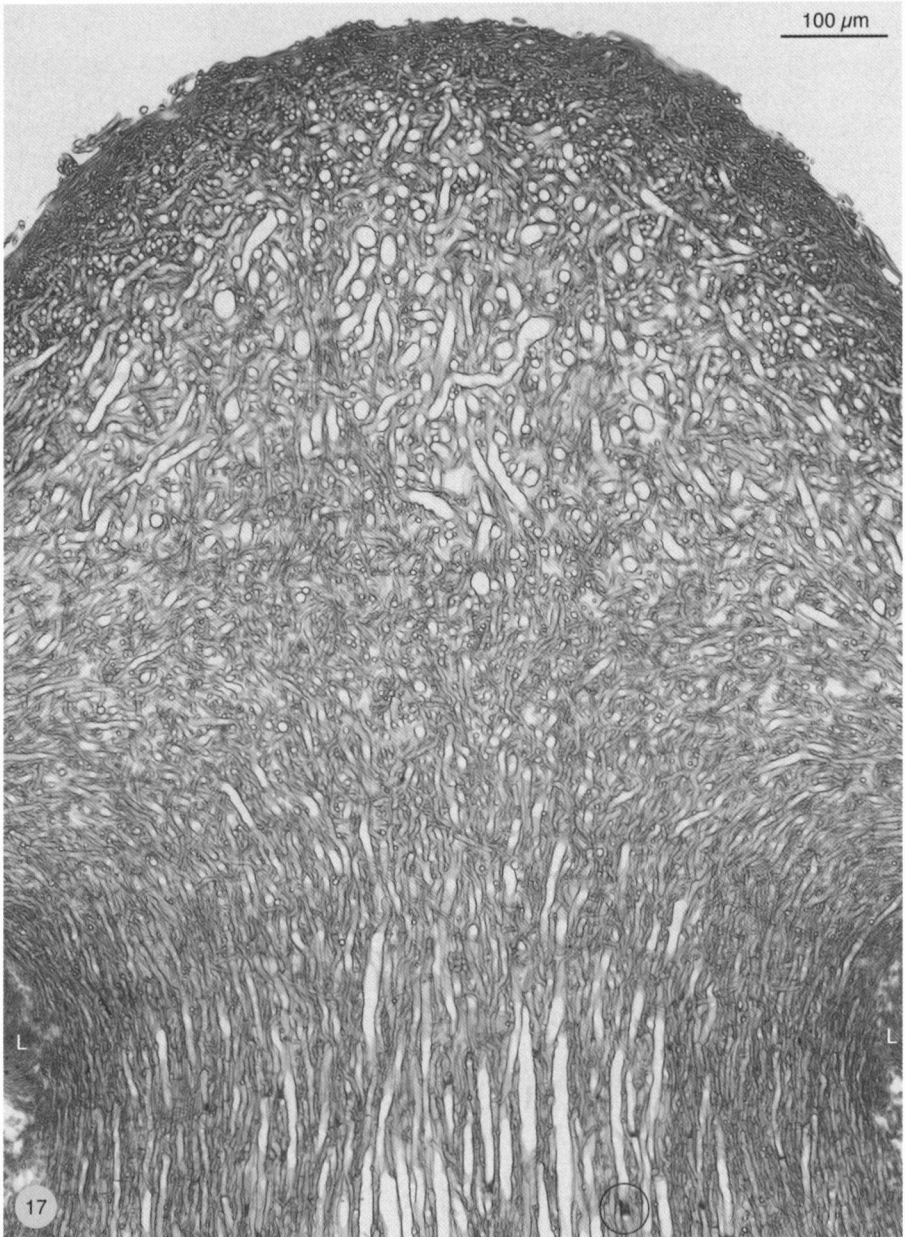
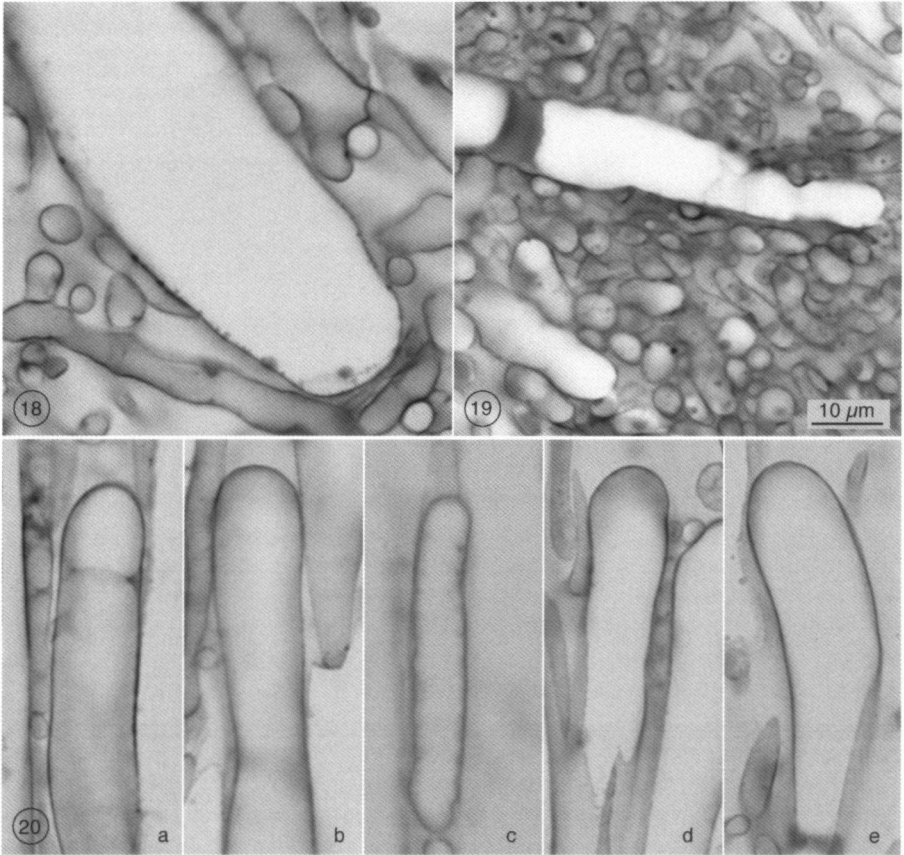


Fig. 16. Formation of the sarcodimitic structure in the stipe. a. Beginning differentiation by vacuolisation of generative hyphae. The white arrow indicates a free end cell reminiscent of acrophysalides; b. an older primordium with more developed physalohyphae which have become strongly inflated and show one or several big vacuoles and cytoplasmic filaments. The nuclei are grouped in small clusters (black arrow).

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 Fig. 17. Median longitudinal section through an old primordium with a strongly gelatinous pileipellis formed by the pileoblema that has become almost completely periclinal. The pileus trama is now strongly sarcodimitic, but the physalohyphae are irregularly arranged. The stipe trama is regularly sarcodimitic. The transition zone between stipe and pileus trama consists of very thin, interwoven generative hyphae. Left and right in the lower part the insertion of the lamellae are just visible (L). The dark spots in some physalohyphae of the stipe (one spot indicated by a circle at the base at the right hand side) probably consist of polysaccharides, as they give the characteristic colour reactions with zirconium-haematoxylin and the tannin-iron reaction.





Figs. 18–20. Free ending physalohyphae reminiscent of acrophysalides in an old primordium. 18. In the lower right half of a pileus; 19. in the pileipellis; 20. in the stipe, where they are especially numerous. Scale valid for all figures.

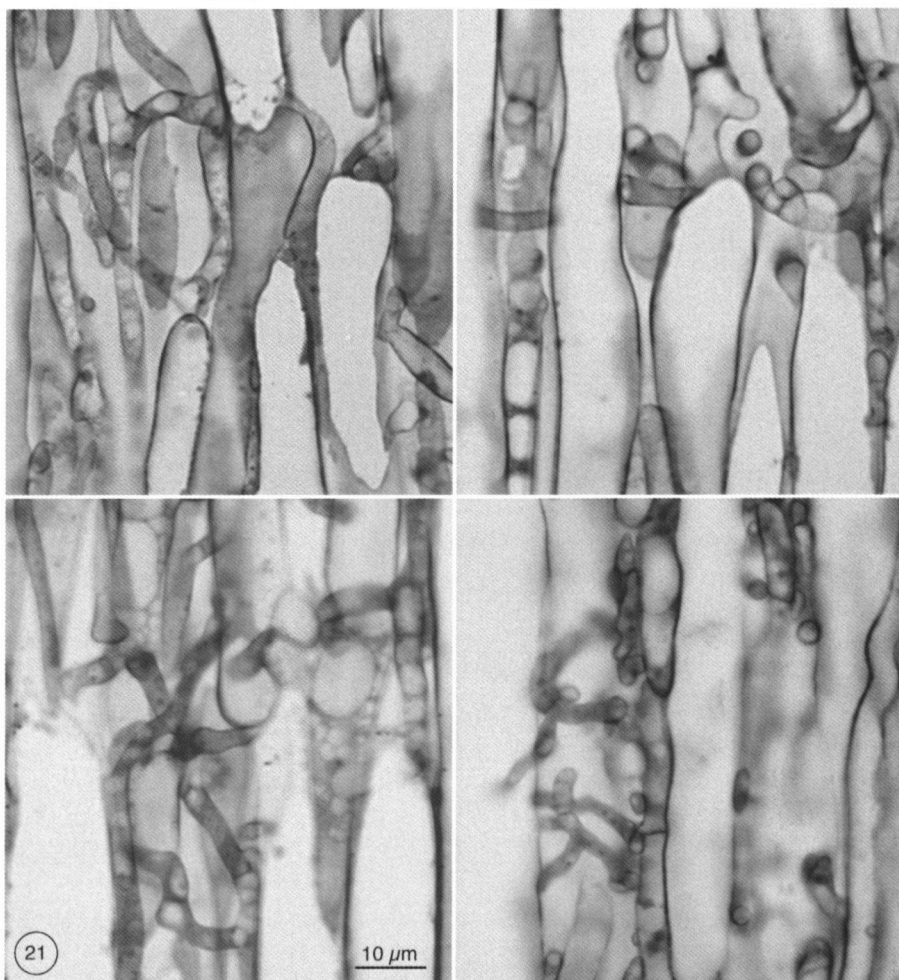
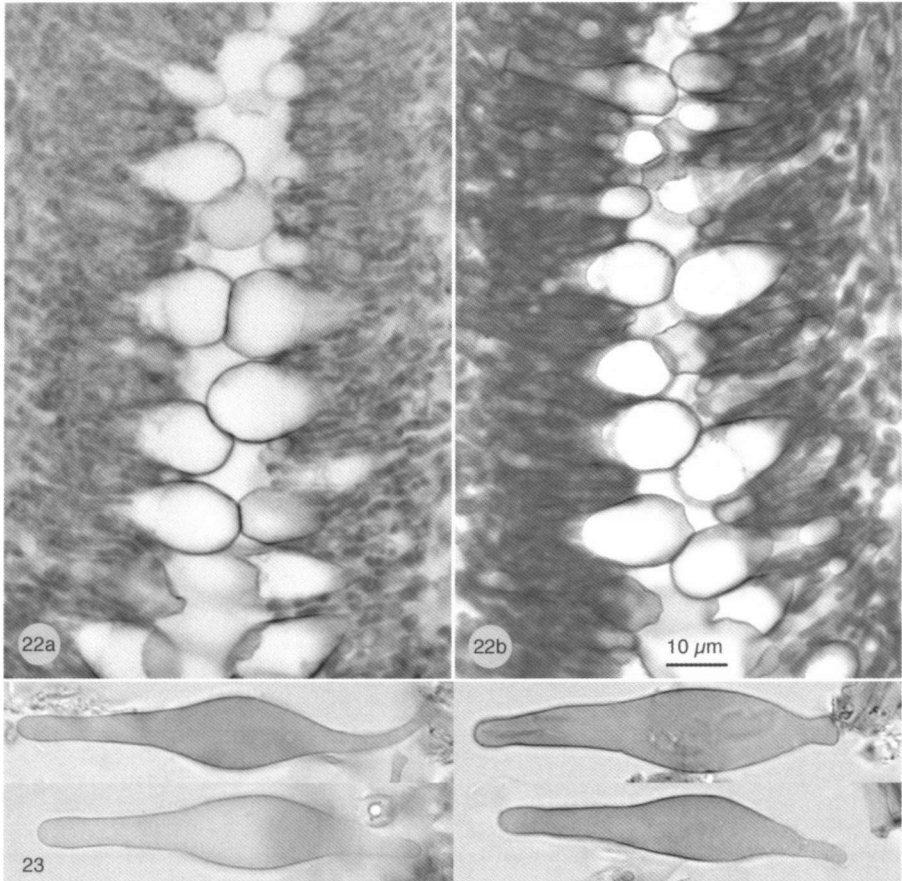


Fig. 21. Thin, strongly ramified 'connective' hyphae between the wide physalohyphae probably lend some mechanical cohesion to the stipe. They are binucleate and clamped. Scale valid for all figures.

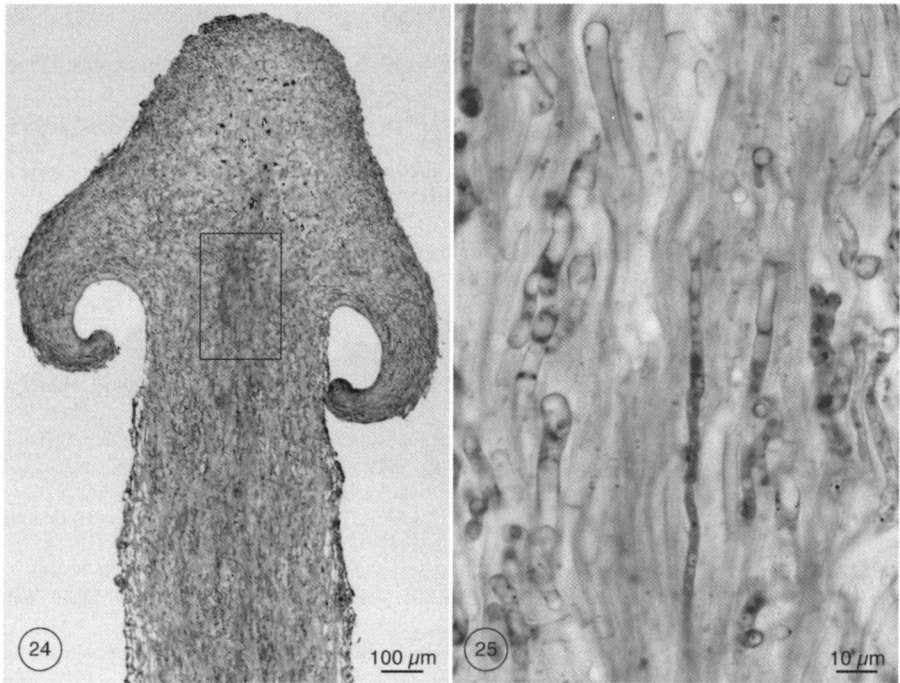


Figs. 22a, b. The space between two neighbouring gills of an older primordium is spanned by very numerous bridging vesicular cystidia that are not lageniform. It is possible that the cystidial bridges have a morphogenetic function by holding the gills in place during cap growth or expansion.

Fig. 23. Free hymenial cystidia of a mature basidiome, shown at the same magnification as the bridging cystidia in Fig. 22.

In some specimens, the pileoblema of erect hyphae changes much earlier into a primordial cortex or into an ixocutis, than in other specimens. The primordium of Fig. 8 is younger than that of Fig. 11, yet its pileoblema is already reduced. Probably this depends on the immediate surrounding of the primordium; narrow contact with the soil may accelerate the transformation.

The development of *Hydropus subalpinus* is reminiscent of the carpogenesis of *Baeospora myosura*, which forms similar metablemas and a spurious false veil (Cléménçon, in press). The main differences are the much earlier differentiation of the sarcodimitic structure and the less pronounced and more fugacious veil in *Hydropus subalpinus*. Both genera are phylogenetically closely related sister groups (Hibbett & Binder, 2002; Moncalvo et al., 2002). Developmental morphology confirms molecular taxonomic conclusions.



Figs. 24, 25. Aborted primordium lacking the sarcodimitic structure and the expansion pressure it would create. 24. The hyphae of the marginal pileoblema inflate by turgescence and cause the cap margin to curl excessively, sometimes even touching the stipe. Normal primordia are not claustropileate, i. e. they do not create a secondary prehymental cavity by pressing the cap margin against the stipe. The prehymental palisade is dead, and the cauloblema is degenerate. The gray area marked by a rectangle is strongly gelatinous. 25. A detail from the gelatinous zone showing surviving generative hyphae and the absence of physalohyphae. The photographs indicate a morphogenetic function of the sarcodimitic architecture; its lack is fatal.

The high frequency of nematodes in aborted primordia suggests that the nematodes feed on the fungus. They may secrete a substance that increases the permeability and/or decreases the mechanical resistance of the hyphal walls for easier feeding, thus provoking the collapse of the turgescent physalohyphae. This hypothesis remains to be tested, because the nematodes could also be attracted by the primordia already aborted.

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